Ecology and Distribution of Some Pelagic Hyperiidea (Crustacea, Amphipoda) from New Zealand Waters

B. M. BARY[1]

THE MARINE pelagic Amphipoda recorded from New Zealand have been discussed systematically (Stephensen, 1927; Barnard, 1930, 1932; Hurley, 1955), but few data are available on their distribution and ecology. The situation in Australia (Barnard, 1931; Dakin and Colefax, 1933, 1940) and South Africa (Stebbing, 1910; Barnard, 1916, 1925, 1940) is similar. However, in antarctic latitudes some features of the ecology of amphipods have been fairly extensively treated (Mackintosh, 1934, 1937; Hardy and Gunther, 1935).

The data presented herein are of collections made from the survey-frigate H.M.N.Z.S. "Lachlan," in southern New Zealand waters, during the summer of 1951. The hyperiids from these collections have been identified by D. E. Hurley, who generously undertook this taxonomic study (Hurley, 1955).

Fourteen species were present in the collections. Seven of these were new records for New Zealand. Five species, namely, *Parathemisto* (*Euthemisto*) *gaudichaudii* (Guer.), *P. australis* (Stebbing), *P. gracilipes* (Norman), *Cyllopus magellanicus* Dana, and *C. macropis* Bovallius, were present in sufficient numbers to permit discussing some features of their ecology, especially their relationships to the water masses in the area about southern New Zealand. The remaining nine species were of rare occurrence, although their biological and environmental associations provoke discussion.

ACKNOWLEDGMENTS

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MATERIAL AND METHODS

Details of the areas from which collections were made, the gear and the methods, are discussed elsewhere (Bary, 1956, 1959). The areas sampled extended between Wellington and Dunedin (one cruise in January, a second in March, 1951), between Dunedin and Foveaux Strait (during January through March), and between Wellington and Auckland and Campbell islands, about 400 miles south of New Zealand (one cruise, November, 1951). (See Figs. 5, 6.) Procedure and gear were standardized: tows were of 3 minutes at 1½ to 2 knots, within the surface metre of water, using a net of graded silks, 50 cm. in diameter. Of the 80 samples, those of Stations 74–85 were collected whilst the ship was at anchor overnight in a tidal stream in western Foveaux Strait (Bary, 1956). Although the temperature was taken at each of these, salinity was determined only for Station 79. Therefore, only this station is shown in the various figures. All of the rare species collected at Stations 74–85 are shown as being captured at Station 79 in Figures 2, 5*a*. Of the common species, only those captured at Station 79 are illus-

[1] New Zealand Defence Scientific Corps, c/o Navy Office, Wellington, N.Z. Now at Oceanographic Laboratory, 78 Craighall Road, Edinburgh 6, Scotland.
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trated. All samples have been quantitatively analysed.

The method of the temperature–salinity–plankton (T–S–P) diagram (Bary, 1959) is used here to elucidate the distributions of species. Occurrences of species are plotted in the intercepts of the temperatures and salinities of the stations at which they were captured. Species are thus related to the hydrological conditions as indicated by these properties. The water-envelope (Figs. 1–4) surrounds the intercepts of all the temperatures and salinities of the surface waters in the sampled areas, but Figure 1 shows only those for plankton stations. The hydrology of the area and the relationships of these waters are illustrated and discussed by Bary (1959).

T–S–P diagrams of the five commonly occurring amphipods are shown in Figures 3 and 4. The geographical distributions of these species in relation to temperatures (Figs. 5, 6) are discussed and interpreted in the light of information derived from the T–S–P diagrams. The stations have been subdivided into several series, and each of these is as near as possible a synoptic series and a geographic unit. The geographical distribution of the subantarctic species and the coastal–subtropical species are charted for each series. Rare species are charted according to the water properties with which they are associated in the T–S–P diagram (Fig. 2). Thus, *Vibilia stebbingi* (?), at Station 210, is shown to be in water of subantarctic origin in the T–S–P diagram; therefore, the appropriate geographical chart is that which concerns other subantarctic species (Fig. 5*g*). As well, the rare species are listed in Table 1 and appreciations are made of their distributions as recorded by other investigators, and as indicated by the relationships exhibited in the T–S–P diagrams. In the charts they are shown together at Station 79 among the subtropical species.

DISTRIBUTION

Indicator groups of species were selected previously (Bary, 1959) for coastal water (one group), for water originating in the subtropical region (one group), and for the subantarctic region (two groups, a Southern Group for cold water, and a Northern Group for that cold water which has undergone a temperature increase in its progress northward). The cohesion of each of these groups in the T–S–P diagrams can only be interpreted as being due to a correlation between the distribution of the individual species composing the group and the properties of the water body which they inhabit and of which they are indicators. The area of chief concentration of each indicator group of species is shown in Figure 2 by lining-in; there are, however, no species of the Northern Group among the Amphipoda. The stippled arrows indicate the routes (within the diagram) along which oceanic species are believed to be penetrating towards coastal waters. These routes closely coincide with the direction of water movements as deduced from the corresponding T–S diagram of the surface waters (Fig. 1).

The cold-water Amphipoda are represented solely by species of the Southern Subantarctic Group (Fig. 3). Large numbers of *Parathemisto* (*Euthemisto*) *gaudichaudii* were captured; there were fewer specimens of *Cyllopus magellanicus*, and *C. macropis* was rare. Both the numbers of these oceanic species, and the frequency of their occurrences decreased in coastal waters, probably as a result of their being transferred into relatively adverse conditions. However, the greater number of the stations in coastal waters were occupied in daylight (Fig. 1) which may contribute towards the taking of fewer specimens (this feature is discussed by Bary, 1959).

The occurrences of two Coastal species, *Parathemisto gracilipes* and *P. australis*, and of the subtropical species, *Hyperoche mediterranea* Senna, are shown in Figure 4. *Hyperoche mediterranea* is restricted to a narrow range of temperature in the warmest waters (except for Station 100) whilst *P. gracilipes* and *P. australis* occur commonly over much the same salinities, but over a wider range of temperatures.

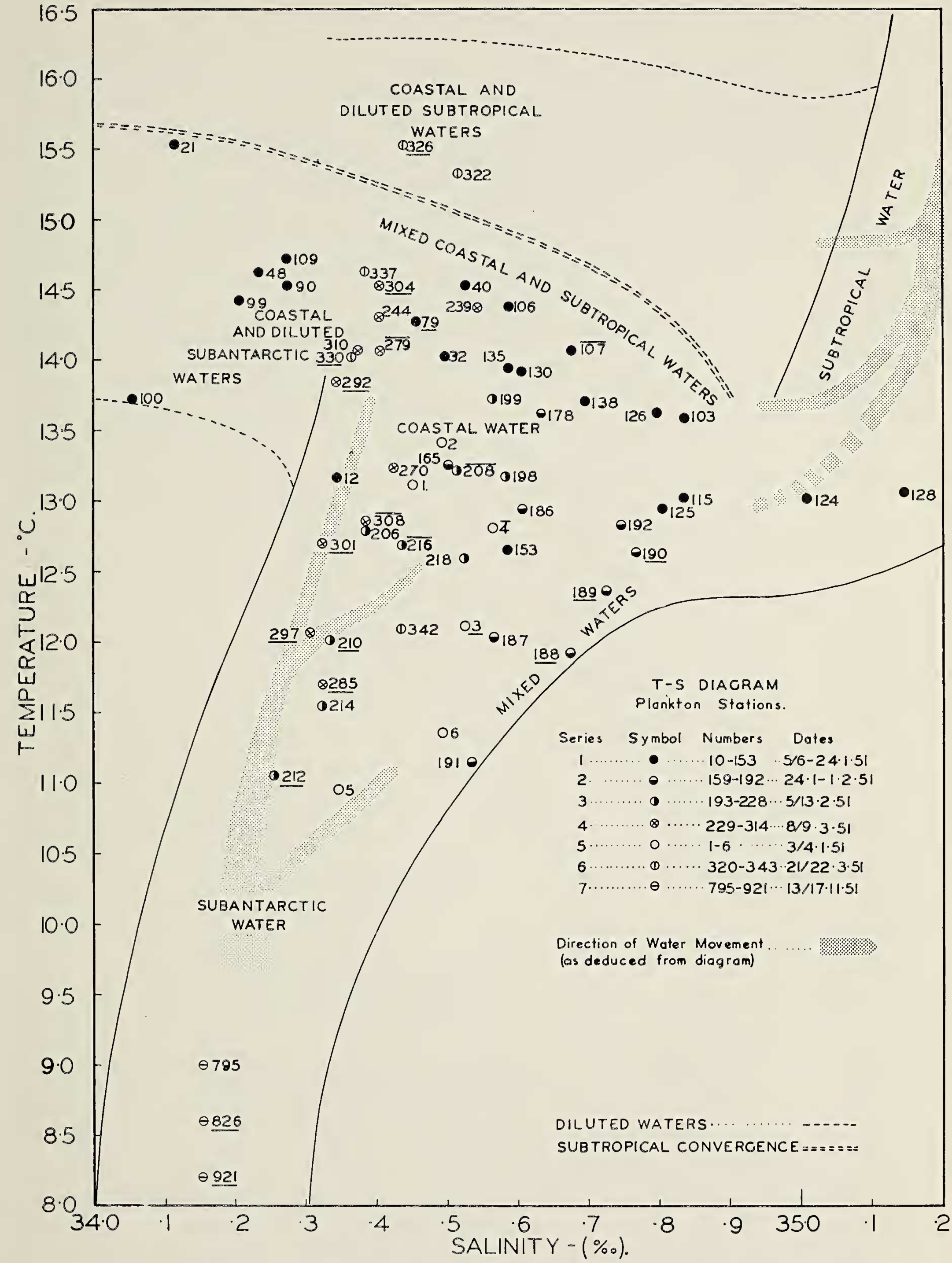


FIG. 1. Temperature–salinity (T–S) diagram of surface waters about eastern and southern South Island, New Zealand, extending southwards to Auckland and Campbell Islands. Plankton stations for which temperatures and salinities were obtained are entered. Numbers underlined (e.g., 212) represent night stations; numbers overlined represent stations between dawn and sunrise or sunset and dark. Stations without lines were occupied in daylight.

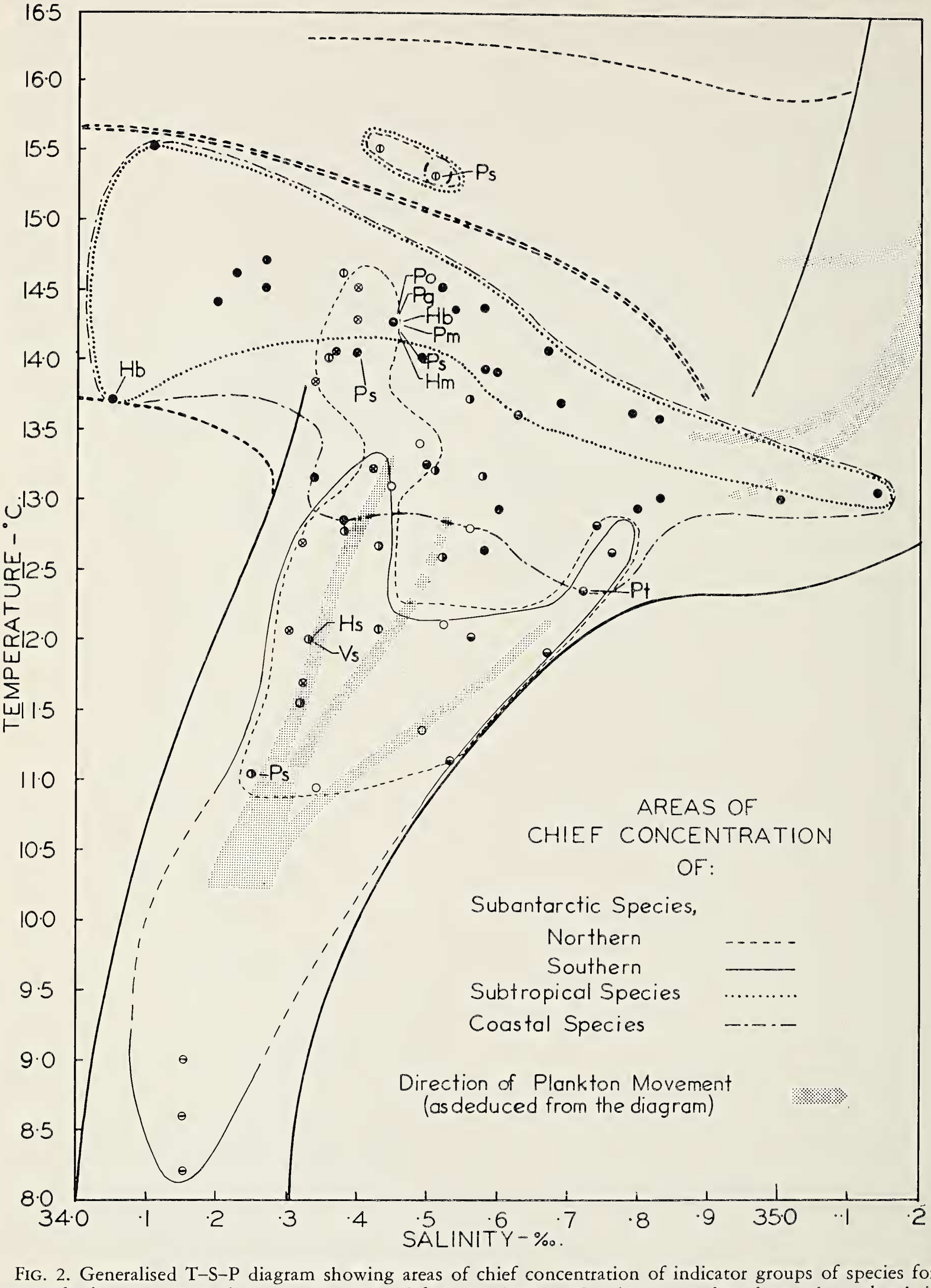


FIG. 2. Generalised T–S–P diagram showing areas of chief concentration of indicator groups of species for waters of subtropical and subantarctic origins and for coastal waters. Species captured rarely are shown by their initial letters adjacent to the station at which they were captured (see text for Station 79). *Po* = *Platyscelis ovoides*. *Pg* = *Paralycaea gracilis*. *Hb* = *Hyperia bengalensis*. *Pm* = *Primno macropa*. *Ps* = *Phronima sedentaria*. *Hm* = *Hyperoche medusarum*. *Pt* = *Parascelis typhoides* (?). *Hs* = *Hyperia spinigera*. *Vs* = *Vibilia stebbingi* (?).

The species discussed normally inhabit waters of a restricted and specified range of properties. However, the subantarctic species *Parathemisto gaudichaudii* and *Cyllopus* spp. and the Coastal species *P. australis* and *P. gracilipes* occur together at Stations 308, 292, 330, 310, 279, and again at Station 189 (Figs. 1, 2); again, the subtropical species *Hyperoche mediterranea* and the coastal species *P. australis* and *P. gracilipes* occur at Station 79. These collections of amphipods of mixed origin are present along with other species belonging to one or more of the several indicator groups of species. This is interpreted as evidence that the waters in which the species are habitually present are mixing together.

The water movements in the area have been deduced from the combined evidence of distributions of salinities, temperatures, and the zooplanktonic indicator species. They are discussed in detail elsewhere (Bary, 1959), but the isotherms of Figures 5 and 6 serve as a basis to recapitulate the main features. Briefly, there appears to be a moderately strong influence from water of subtropical origin which extends from the west into Foveaux Strait and can be traced around the coast to Dunedin and beyond. It is probable that some water of subantarctic origin, mixed with the subtropical water, also enters the Strait from the west. Water of subantarctic origin periodically penetrates in smaller or larger intrusions into the waters in the Strait and coastal areas. These several waters mix to form one of intermediate properties which is designated herein as "coastal water" (Fig. 1). It is believed probable that only water of subantarctic origin is present at Stations 826 and 921 of Series 7, and possibly also at Station 725 (Figs. 1, 6*c*). Data from stations of Series 5 and 6 (Fig. 6), together with those from a surface thermograph trace made two weeks later, on a course parallel to and seaward of the stations of Series 6, indicate the location of the subtropical convergence. It was not crossed by "Lachlan" in January when it was probably to the north of Station 1, but it was present a little northward of Station 330 in March (Series 6).

With the species of Amphipoda related to their respective waters by the T–S–P diagrams, their presence or absence at a station becomes significant in that there is an indication of the waters present. The subtropical species *Hyperoche mediterranea* is confined to that portion of Foveaux Strait likely to be most directly influenced by water of subtropical origin (Fig. 5*a*). The coastal species *Parathemisto australis* and *P. gracilipes* occur along with *H. mediterranea*, but in all series they occur over a larger area, and a wider range of temperatures. From Figure 5*a* to *d*, it is clear that neither subtropical nor coastal species penetrate into areas where the influence of water of subantarctic origin is strong, e.g., Stations 210 to 218 (Fig. 5*c*, *g*), or 285, 297 (Fig. 5*d*, *h*). On the other hand they are found, together with subantarctic species, at those stations in the mixed waters immediately northeast of Stewart Island (Fig. 5*a*, *e*) and more especially at Stations 187, 189 (Fig. 5*b*, *f*), 208 (Fig. 5*c*, *g*), 279, 292, 308, 310 (Fig. 5*d*, *h*), and again at Station 330 (Fig. 6*d*, *e*). In the T–S diagram (Fig. 1) these stations (except 187, 189) are seen to extend as a group between water of subantarctic origin and coastal water. In the T–S–P diagrams Figures 2, 3 the occurrence of the subantarctic species of plankton at all of these stations emphasises a certain affinity between them; it would seem that they are directly within the influence of water of subantarctic origin. This is confirmed by the geographic charts, which suggest that although some of the stations are located in inshore waters each, in fact, is located in the vicinity of tongues of colder water penetrating shorewards. This is especially so for Stations 279 and 292, less so for Station 208. Stations 308 and 310 appear to be in waters that are more generally mixed, but into which water of subantarctic origin appears to be intruding, particularly about Station 297 (Fig. 5*d*, *h*). Stations 187 and 189 (Fig. 5*b*, *f*) are also located near intruding

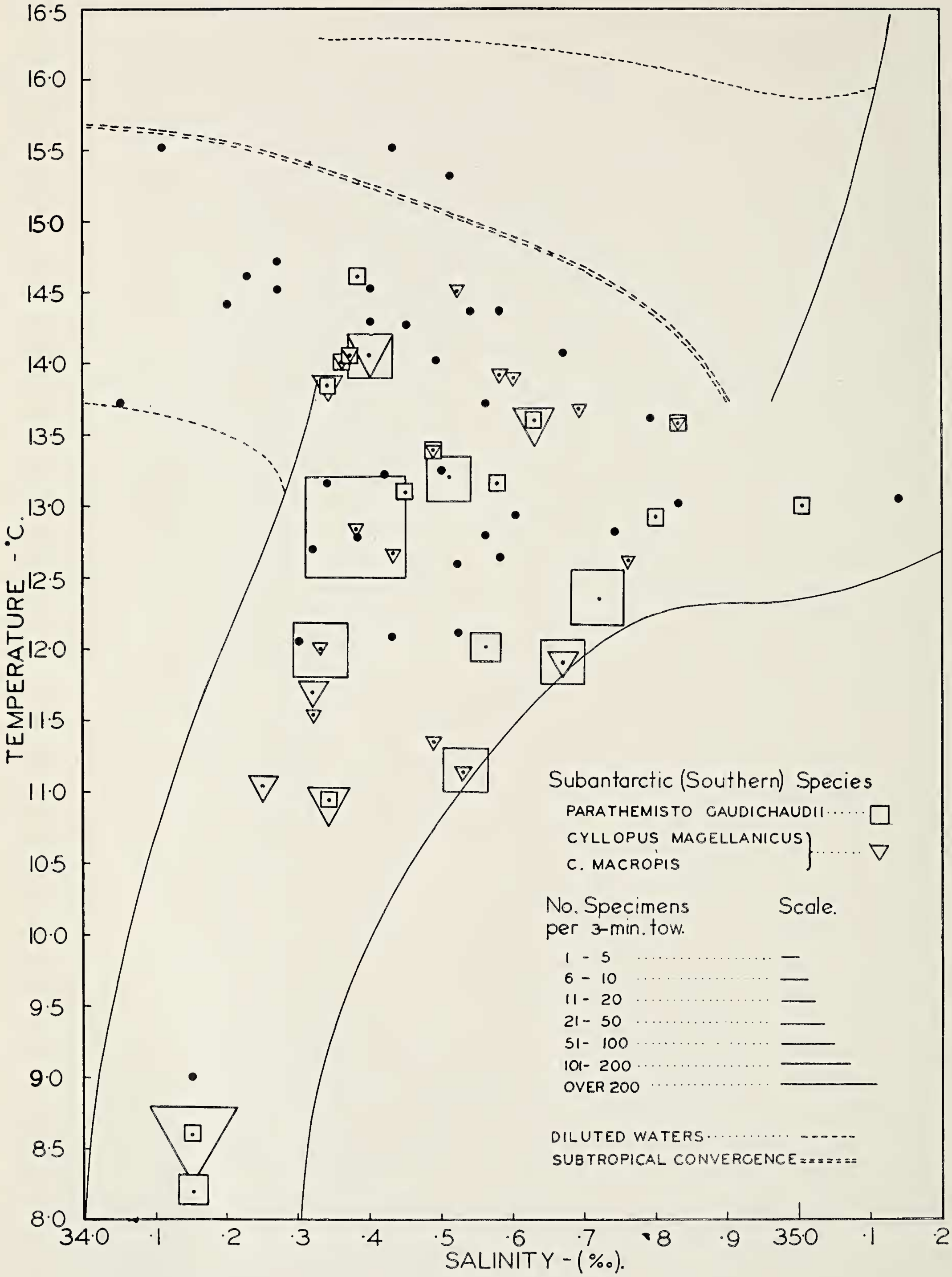


FIG. 3. Temperature–salinity–plankton (T–S–P) diagram of the species of Amphipoda associated with water of subantarctic origin.

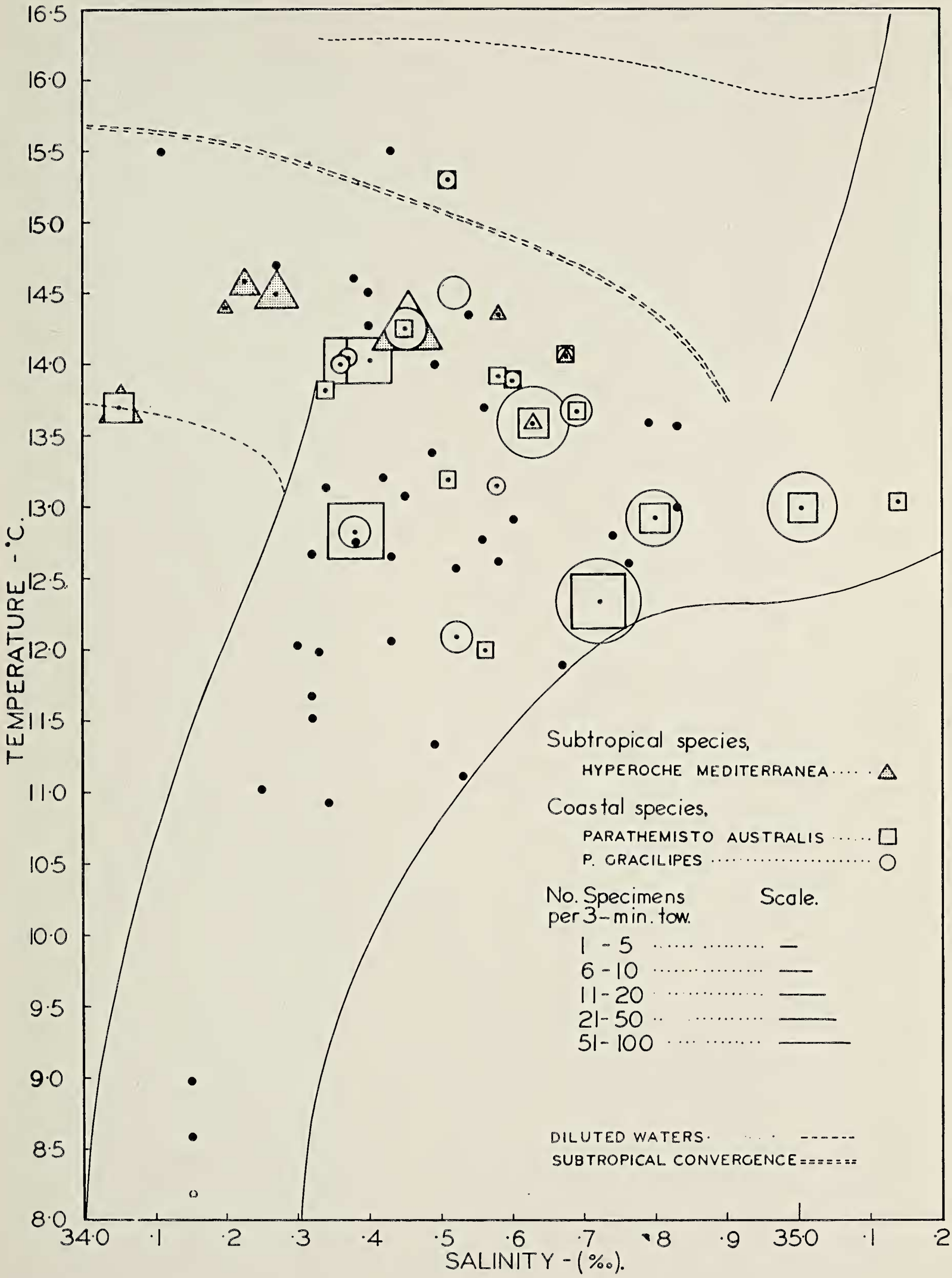


Fig. 4. T–S–P diagram of the species of Amphipoda associated with water of subtropical origin, and with co:stal waters.

subantarctic water, and again the mixture of species results. At these stations there is a slightly stronger influence of coastal water than in the previous examples, as shown by higher salinities (Fig. 1). The absence of any subtropical species at 187 and 189 suggests little influence from water of this source.

The isotherms for January (Series 5, Fig. 6*a*, *b*) indicate that water of subantarctic origin extends at least to Cook Strait. One or both of the subantarctic species *Parathemisto gaudichaudii* and *Cyllopus magellanicus* are present at four of the six stations. They are absent from Stations 3 and 4. This, together with salinities which are a little higher than in neighbouring subantarctic water (Fig. 1), indicates that those stations are being influenced by coastal water, probably from south of Banks Peninsula. Although this water does not exclude subantarctic species, it supplies a reason as to why *Parathemisto gracilipes* occurs at Station 3 (and also why other species of the Coastal Group were present at both Stations 3 and 4). In Figure 6*d*, *e*, the subtropical convergence transects the series. Subantarctic species are present at Stations 337 and 330; *P. gracilipes* is also present at Station 330, and both *P. gracilipes* and *P. australis* at 322. Station 322, north of the convergence, is in mixed subtropical-coastal waters (Figs. 1, 2) and the occurrence there of a coastal species is consistent. Species from all groups are to be expected at Station 330. It is shown by the mixture of zooplankton to be situated in mixing waters in the T–S–P diagram (Fig. 2), and this is borne out by its geographical location near or within the mixing area between waters originating in the subtropical and subantarctic masses (Fig. 6*d*, *e*).

Perhaps the most important feature illustrated by Figure 6 is that the two subantarctic species, few in individuals though they are, are present only in water believed to have originated in the subantarctic. They act as indicators and demonstrate the northward extent of subantarctic water, as well as demarcate the approximate position of the subtropical convergence in March, 1951.

It perhaps should be emphasised at this point that in the southeast coastal area of New Zealand, where mixed waters of diverse origins predominate, it would be most difficult to disentangle the sources of the waters and the species from charts of distributions alone. Interpretations would be largely deductive and subjective. The T–S–P diagram demonstrates in a clear and effective manner, the source of both the waters and the species in the area. At the same time it provides a means of utilising occurrences of species to follow the trends of water movements. Thus the occurrences of species of plankton at certain localities, and of the means by which they arrived at their point of capture, can be explained with a fair degree of certainty.

Rare species are symbolised in Figures 2, 5, and 6 by their initial letters. Occurrences of one or a few species, on one or two occasions, are often insignificant in distributional studies. In the context of the T–S–P diagram (Fig. 2), however, their occurrences may assist in the interpretation of conditions; conversely, the conditions in which they occur may assist in interpreting other features concerning the species, e.g., see a later discussion of *Parathemisto* spp.

The cold-water species *Hyperia spinigera* is demonstrated as being captured in water of subantarctic origin (Station 210, Figs. 2, 5*g*)—water in which the species is normally resident. *Hyperoche medusarum* Kroyer, another cold-water species, occurs at Station 79 (Figs. 2, 5*a*). This might be regarded as a stray specimen, but the presence of small numbers of other species of the Subantarctic groups, e.g., Copepoda, suggests an intrusion of water of subantarctic origin towards this station. Two species present at Station 79 are of subtropical origin, namely *Platyscelus ovoides* (Claus) and *Paralycaea gracilis* Claus. These, and probably also *Hyperia bengalensis*, are regarded as entering, along with water of subtropical origin, into Foveaux Strait from the west. As would be expected, undoubted cos-

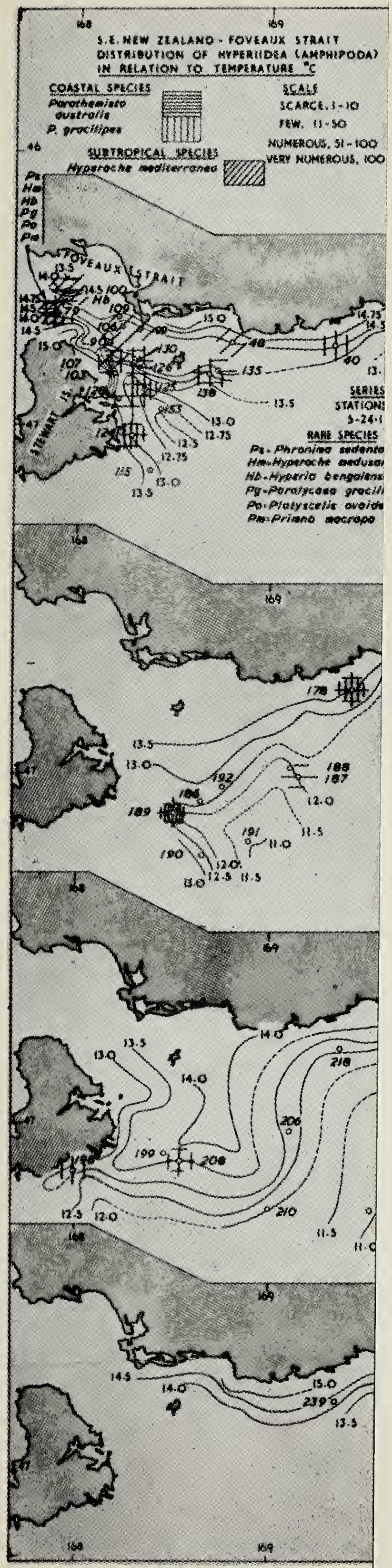


FIG. 5. Charts of distributions of Ampl
separately from Subantarctic species (*e–h*)

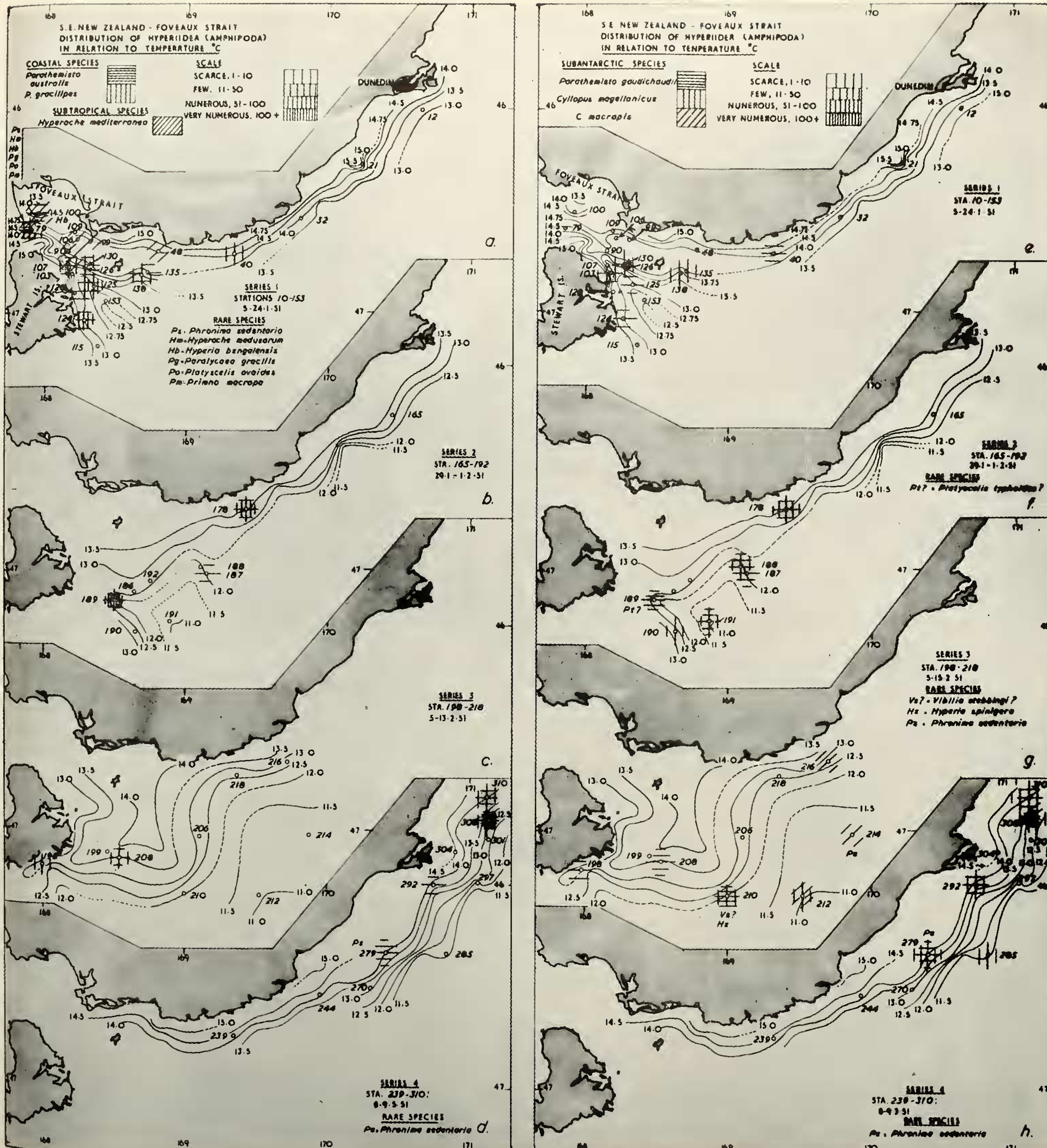
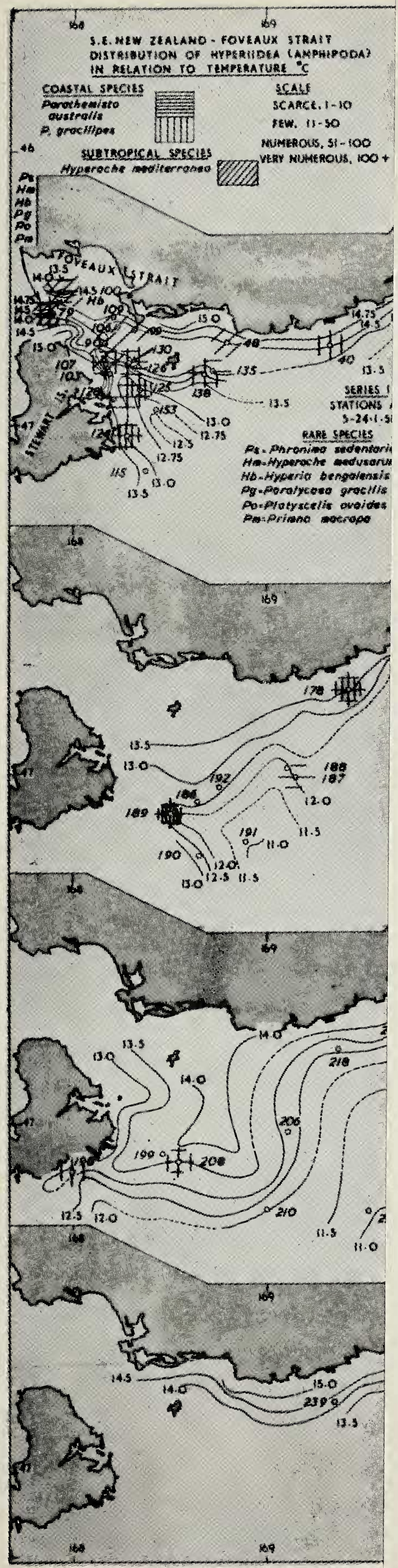


FIG. 5. Charts of distributions of Amphipoda relevant to temperature distribution about Foveaux Strait. Coastal and Subtropical species (*a–d*) are illustrated separately from Subantarctic species (*e–h*) for each series of stations. For a discussion of the rare species, see text.



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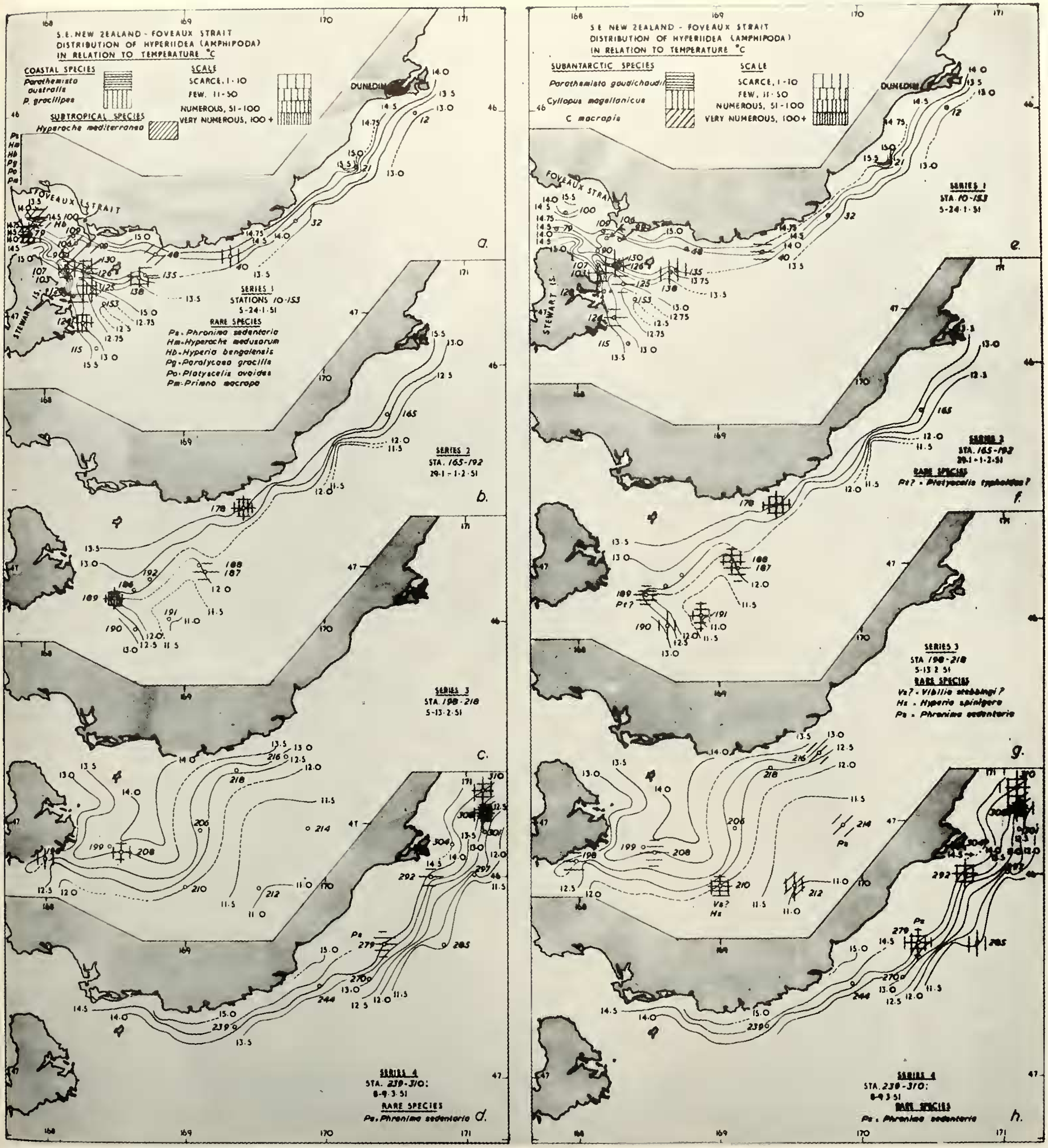

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mopolites may occur at stations located in a variety of waters. Thus, *Phronima sedentaria* (Forskal) is present in water of subtropical origin north of the subtropical convergence (Station 326, Figs. 2, 6*d*), in mixed water (Station 79, Fig. 5*a*), and in water predominantly of subantarctic origin (Stations 214, Fig. 5*g*), or being influenced by this water (Station 279, Fig. 5*h*). *Hyperia bengalensis* (Giles) was present in mixed or diluted coastal waters (Stations 79, 100), and *Primno macropa* Guer., another cosmopolitan species, also occurred at Station 79 (Figs. 2, 5*a*). Thus, on the whole, these species are shown to have been captured in conditions suitable for them. Conversely, their occurrences in conditions consistent with those previously recorded for them adds to the value of interpretations based on the more commonly occurring species.

Two of the New Zealand species listed in Table 1 are regarded as being doubtfully identified (Hurley, 1955). The identification of one, and possibly also of the other species, is not upheld when their relationships to the water masses, demonstrated in the T–S–P diagram, are compared with their previously recorded distributions. *Vibilia stebbingi* (?) Behn and Wolt, is present in water of subantarctic origin (Station 210, Figs. 2, 5*g*) which is out of character with the tropical-subtropical range usually ascribed to this species. *Parascelis typhoides* (?) Claus, another tropical-subtropical species was captured at Station 189 (Figs. 2, 5*f*), believed to be located in a mixture of coastal and subantarctic waters; the absence of any others of the selected Subtropical Group of species indicates little influence at this point from water of subtropical origin. Thus this occurrence of *P. typhoides* (?) may also be anomalous, suggesting again that misidentification is possible.

A comparison of the average numbers of a species captured in coastal and in offshore waters may indicate the degree to which the species penetrate from one water into the other. When numbers captured per haul over a specified range of depth are plotted against depth of water, the commoner amphipod species illustrate that this applies. (See Fig. 7; deeper water in the area of sampling is indicative of an increase of distance offshore and proximity to oceanic water.)

Both *P. gaudichaudii* and *Cyllopus magellanicus* (Fig. 8, unbroken line) show decided increases in the numbers captured from shallow (coastal) to deep water. A fair degree of tolerance to coastal waters is suggested for *P. gaudichaudii* by the almost steady increase in numbers as samples proceed offshore. On the other hand, the sudden decrease in water shallower than 50 fathoms (91.5 m.) shown by *C. magellanicus* is indicative of intolerance to conditions in the coastal water. *P. gracilipes* and *P. australis* (Fig. 7) increase in numbers to a peak at 50 fathoms (91.5 m.), and decrease in the deeper, offshore water. This suggests that neither species is tolerant of conditions in this water (see later). These facts confirm the relationships of the species to water masses already obtained from the T–S–P diagrams (Figs. 2, 3, 4).

The collections of this study were made during a period of three months. During the latter half of this a larger proportion of stations were over deeper water, either directly influenced by, or believed to be situated in water of subantarctic origin. It seemed possible, therefore, that variations in the catches of a species, relative to depth of water, might be reflected in the numbers captured at different times in the three months. So that direct comparisons might be made, the average number of specimens per haul for each month are included in the figures of changes of the catch with depth (Fig. 7 dashed line). *Cyllopus magellanicus* shows an overall decrease in numbers during January through March which is opposed to the increase with depth. Numbers of *P. gaudichaudii* on the other hand, increase with each monthly catch, although less so for March than for January and February. Even so, the number collected

TABLE 1

RARELY CAPTURED SPECIES AND THEIR PREVIOUSLY RECORDED DISTRIBUTION IN RELATION TO THAT SHOWN BY THE T–S–P DIAGRAM

SPECIES	SYMBOLS IN FIGURES	STATIONS COLLECTED	NUMBER OF SPECIMENS	DISTRIBUTION: Recorded in literature	DISTRIBUTION: Summary*	AS FROM T–S–P	AGREEMENT
1. *Vibilia stebbingi ?*	Vs	210	1	Mediterranean; 35°N.–30°S. Atlantic; E. Pacific; N.Z.	ST–T	SA	Poor (possibly misidentified)
2. *Hyperia bengalensis*	Hb	83	14	40°N.–45°S. Atlantic; Mediterranean; Arabian Sea; Cape Howe and N.S.W., Australia; Bermuda	ST–COS	Mixed ST–C–SA	Satisfactory
		100	4				
3. *Hyperia spinigera*	Hs	210	1	North Norway; Labrador current; W. Ireland; S. England; E. mid-Atlantic; S. Georgia; Friday Harbour; N.Z.	Arctic–Subarctic; A–SA	SA	Very good
4. *Hyperoche medusarum*	Hm	75	1	55°–77°N. Atlantic; N. Alaska; S. Georgia; at 1500–3000 m., 19°–35°S. Atlantic; N.Z.	Arctic–Subarctic	Mixed ST–C–SA	Fair
5. *Phronima sedentaria*	Ps	82	1	Mediterranean; 60°N.–36°S. Atlantic; Indo-Pacific; N.Z.	COS	82 Mixed ST–C–SA	Very good
		214	1			214 } SA	
		279	3			279 } SA	
		326	1			326 ST	
6. *Primno macropa*	Pm	74	1	Mediterranean; 30°N.–66°S. Atlantic; Indian; N. Pacific; 58°–66°S. Pacific	COS	Mixed ST–C–SA	Good
		75	1				
7. *Paralycaea gracilis*	Pg	83	1	Mediterranean; 53°N., 47°N., and Trop. Atlantic; 39°S., 140°E., Pacific; N.Z.	T–ST	Mixed ST–C–SA	Satisfactory
8. *Parascelis typhoides ?*	Pt	189	1	N.–S. Atlantic; Mediterranean, Red Sea	T–ST	Mixed SA–C	Poor (possibly misidentified)
9. *Platyscelis ovoides*	Po	75	3	N.–S. Atlantic; Indian Ocean and G. of Aden; Mediterannean	T–ST	Mixed ST–C–SA	Fair

* T—Tropical; ST—Subtropical; SA—Subantarctic; A—Antarctic; COS—Cosmopolitan; C—Coastal.